Experimental colonisation of contrasting habitats by house mice

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Abstract

House mice (*Mus domesticus*) are successful colonists, thriving both indoors and outdoors in a wide range of habitats, with the general exception of woodland. We investigated some of the processes affecting house mouse colonisation success by comparing the fates of mice experimentally introduced into woodland or buildings and provided with food and shelter (straw stacks) at a focal point. House mice introduced into buildings generally became established and bred, while house mice introduced into woodland declined to extinction within three months. House mice in buildings radiated away from the stacks and some established in the surrounding grassland, while house mice in woodland rarely left the stacks. At buildings captures of house mice outdoors correlated negatively with captures of wood mice (*Apodemus sylvaticus*). There was evidence of heavy predation by weasels (*Mustela nivalis*) on house mice in woodland, but not in buildings. We suggest that woodland was unsuitable for house mice due to a combination of competition and predation: competition with wood mice restricted house mice to their focal introduction point making them vulnerable to extinction through predation by weasels.

Introduction

Colonisation can be defined as a process which starts with the arrival of a propagule in a new habitat patch, and ends when the probability of extinction is no longer dependant on propagule properties (Ebenhard 1991). The house mouse (*Mus domesticus*) is a highly successful colonist, being one of the most widespread of all mammals (Meehan 1984). There are few studies relating specifically to colonisation of house mice, but the unsuccessful attempts of Berry et al. (1982) to introduce them to the Shetland Isles suggest that even for this species, colonisation is not always a simple process.

House mice have become established in an enormous range of environmental conditions, living both ferally and commensally (Berry 1981). Woodland, however, is one habitat in which records of house mice living independently from man are scarce throughout the world. An exception is woodland in New Zealand, where no other small rodents are present (Fitzgerald et al. 1981; King 1982), but even these house mouse populations live at very low densities (0.6–3.3 per hectare). House mice have adapted to almost every conceivable climate (Berry 1981) and so it is unlikely that they are prevented from colonising woodlands by an abiotic variable.

In southern England several factors could prevent house mice from colonising woodland. For example, they might not range widely enough to encounter woodland sufficiently regularly, and are unlikely to be translocated there by man. We investigated some of the processes affecting colonisation success of house mice introduced into favoured habitat (buildings) and into apparently sub-optimal habitat (woodland). Using live-trapping we aimed to discover whether there were habitat-related differences in survival, breeding, and expansion, and whether these were mediated by predation or competition.

Material and methods

Study sites

Building sites were situated at a semi-derelict farm and horticultural station near Shinfield, Berkshire, UK. Outdoor sites were in University of Reading woodland near Shinfield, Berkshire, UK. Sites in buildings ranged from a small tin-roofed building, to an old stable block, to old chicken houses. All buildings were surrounded by rough grassland, concrete, and other buildings. Woodland areas were predominantly mixed deciduous and coniferous, with some hazel (*Corylus avellana*) coppice. House mice were not present at any site prior to the experimental releases, but there was movement of small numbers of experimental animals between nearby building sites both within and between trials. Wood mice (*Apodemus sylvaticus*) were present at all sites, but not inside buildings.

Experimental releases

Eighteen groups of three male and nine female house mice bred from wild stock were individually marked by toe-clipping under Home Office licence, and one group was released into each of 18 straw stacks. Stacks were built with 12 bales of straw, and measured 1.5 m by 1 m around the base and 2 m high. Nine stacks were in derelict buildings and nine stacks were in woodland.

Releases of house mice took place in three trials (May 1991, November 1991, and March 1992), each using a different three building stacks and three woodland stacks. For each trial, the introduced animals were adults taken from the same stock and matched for sex and, so far as possible, for weight, in paired building and woodland stacks. However, the degree of relatedness, and the degree of social contact between animals introduced into a particular stack was not always known, and probably varied. Fighting among introduced males in particular would have been reduced if males had been housed together prior to release, or if they were siblings.

In all trials, pups up to two days old were introduced with their mothers because most of the other, non-suckling, females were heavily pregnant. Large numbers of pups were introduced in May (32 in buildings and 52 in woods); in November and March no more than 15 pups were introduced. Evidence considered later suggests that few of these extra individuals survived.

As well as an initial 1 kg of wheat scattered inside the stack, animals were provided with 1.75 kg wheat ad libitum from a covered food box placed next to the stack. This was renewed approximately every three weeks, and became depleted only in woodland stacks.

Monitoring

Changes in populations of house mice and naturally occurring wood mice were followed using Longworth live traps and capture-mark-release methods. The areas in and around the stacks were trapped both before and after introduction, at approximately three to four-week intervals until house mice were no longer being captured (9–23 weeks). Sixty traps were used: eight in and under the stack, four around the food box, a square of eight 1 m from the stack. The remainder were placed in three concentric squares consisting of eight, 16, and 16 traps, placed 5 m, 15 m and 20 m from the stack, with distances between traps of 5 m, 5 m, and 10 m respectively. This layout was adhered to as strictly as possible, but physical constraints imposed by walls meant that layout in buildings varied. Trapping sessions lasted for three nights. Within each trial, timing of introduction and trapping was exactly paired for building and woodland stacks.

Statistical tests

House mouse and wood mouse abundances were calculated as Minimum Number Alive (MNA). Newborn pups could not be included in these analyses until they became large enough to be captured and marked, at least three weeks after their introduction. In order to combine information from different trials data were tested for homogeneity using Chi-squared.

At each site we used regression analysis to calculate the slope of the change through time in numbers of all individuals and in numbers of original colonists. The total number of house mice at day 0 was the number introduced, that is, 12, and this number was excluded from the regression analysis for total

MNA, as a known number of mice was not comparable with an estimated number. The sudden drop in the number of house mice estimated one day after introduction in May supports this exclusion. The slopes of changes in numbers in buildings and woodland were compared by analysis of variance; sources of variation were habitat (building or wood) and month (May, November, and March).

We used body weight as a predictor of age, and divided all non-original individuals caught in a stack into three groups: (a) conceived in stack, (b) introduced into stack as a pup or as a foetus, and (c) migrant from an experimentally introduced population at a nearby stack. For example, 36 days after introduction, individuals conceived in the stack weighed less than 6 g, while those introduced into the stack as pups or foetuses weighed 7–10 g. Adults introduced into the stack weighed more than 15 g. Best estimates of numbers in each group took into account trap position (central or peripheral) and all weight recordings. Maximum and minimum estimates were produced by inclusion or exclusion of animals with first recorded weights on the borderline of one of the three groups. Data (in the form of counts) remained separate for each stack, and were transformed with a square root transformation prior to an ANOVA test. ANOVA was performed separately on best, maximum, and minimum estimates for individuals conceived, introduced, and total produced, with month (May, November, and March) and habitat (building or wood) as sources of variation.

At each site we calculated the proportion of all house mouse captures which occurred away from the stack, and the proportion of individuals which occurred away from the stack. We define 'away from the stack' as excluding traps in the area inside or under the stack, and the four traps around the food box. These proportions were then transformed using an angular transformation prior to ANOVA. Sources of variation were habitat (building or woodland) and month (May, November, and March). A similar analysis for wood mice used the presence or absence of house mice as a source of variation.

Results

Changes in numbers

The Minimum Number Alive (MNA) for house mice and wood mice was estimated at each site for each trapping session (Fig. 1). Using homogeneous data, after 10 days significantly more original colonists remained at woodland sites (83%) than building sites (39%; $X^2 = 30$, df = 1, p < 0.001). After 64 days, however, more original colonists remained in buildings (32%) than in woods (6%; $X^2 = 16$, df = 1, p < 0.001).

There was a significant difference in the slopes of change in total numbers of house mice in buildings and woods ($F_{(1,12)} = 22.7$, p < 0.001), with building slopes tending to be positive (mean slope = 0.01), and all woodland slopes being negative (mean slope = –0.11). Month of introduction had no effect on the slope, and there was no interaction between habitat and month.

Among original adult colonists only, ANOVA again showed that month had no effect, and there was no interaction between month and habitat. The effect of habitat, however, was again significant ($F_{(1,12)} = 11.44$, p < 0.01), with numbers in buildings declining less rapidly (mean slope = –0.06) than numbers in woodland (mean slope = –0.12).

Analysis using data only for original house mice was necessary because some captures on the building sites originated from previous introductions. It was also important to know whether differences in slopes of numbers of individuals arose from adult survival, from survival of pups introduced with their mothers, or from breeding success. The fact that both total numbers of individuals and numbers of original colonists declined faster in woodland than buildings suggests that adult survival was higher in buildings.

Production of young

There was no effect of habitat or month on the total number of individuals produced at each site, or on any estimate of numbers introduced as a pup or foetus. However, all estimates of numbers conceived in stacks showed an effect of habitat, with fewest individuals conceived in woods (for the best estimate $F_{(1,12)} = 8.35$, p = 0.014; for the maximum estimate $F_{(1,12)} = 8.69$, p = 0.012; for the minimum estimate $F_{(1,12)} = 5.11$, p = 0.043).

a) woodland sites
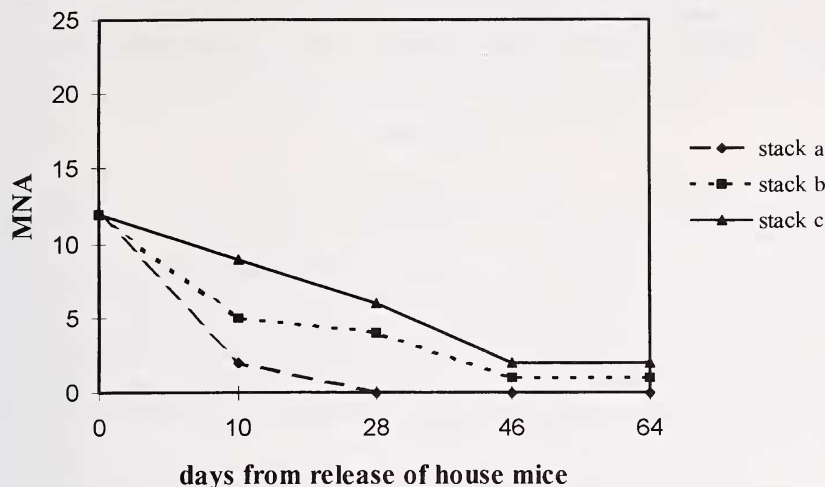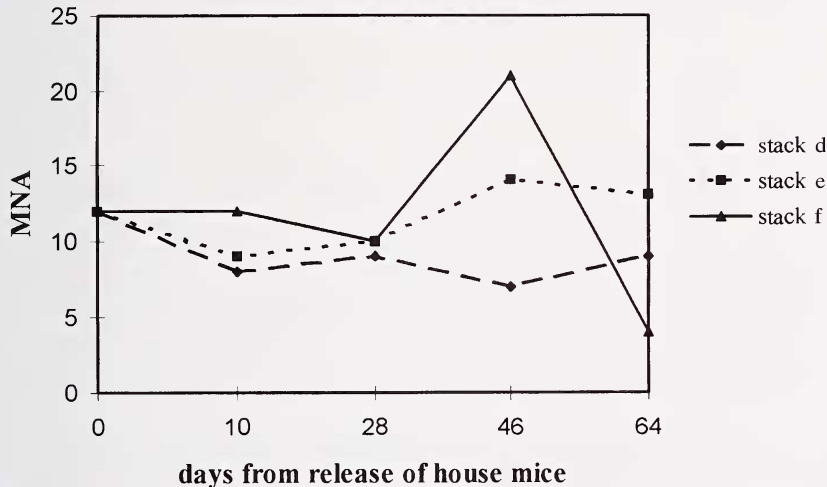

b) building sites

Fig. 1. Minimum Number Alive (MNA) estimates for house mice present at trapping sessions at
a) woodland and b) building sites, using the November trial as an example. The number of house mice
at day 0 was the number of adults introduced, that is, 12.

Equivalent numbers of young were, therefore, introduced as foetuses or pups to build-
ings and woodland and so growth of these extra individuals cannot account for differences
in the rates of population change in the two habitats. The lack of differences between
months, despite the fact that many more mice were introduced as pups or foetuses in May
than in November or March, suggests that few of these extra individuals survived.

Range expansion

Habitat had a significant effect on proportions of both individuals and captures away
from the stack ($F_{(1,12)} = 14.5$, p = 0.003 for individuals; $F_{(1,12)} = 15.8$, p = 0.002 for cap-
tures). There was a greater proportion of both captures and individual house mice caught

away from the stack at building sites (captures: 33.8%, n = 355; individuals: 54.4%, n = 136) than at woodland sites (captures: 7.1%, n = 411; individuals: 19.8%, n = 106) suggesting that expansion from the focal introduction point was greater in buildings than in woodland.

Wood mice

Wood mice were present at all sites, and were most abundant in November. No wood mice were caught inside the buildings, but they were caught around the outside edges of buildings. Overall, the average MNA at any one time at building sites (6.5) was slightly less than that in woods (9.2). However, wood mice on building grids had fewer traps available to them, because many traps were inside the buildings, and because the total building grid area was often less than total grid area in the woods as a result of constraints of trapping in and around buildings. Wood mouse populations outside buildings were, in fact, probably more dense than wood mouse populations in woodland: an average of 0.20 wood mice per trap-night (i. e. per trap outdoors per night) were caught at building sites, compared with an average of 0.15 in woodland.

At seven buildings surrounded by vegetation, there was a negative correlation between the number of captures of house mice and the number of captures of wood mice (r = –0.945, df = 5, p < 0.01) in traps placed outside the buildings (Fig. 2). At most sites there were more captures of wood mice than house mice.
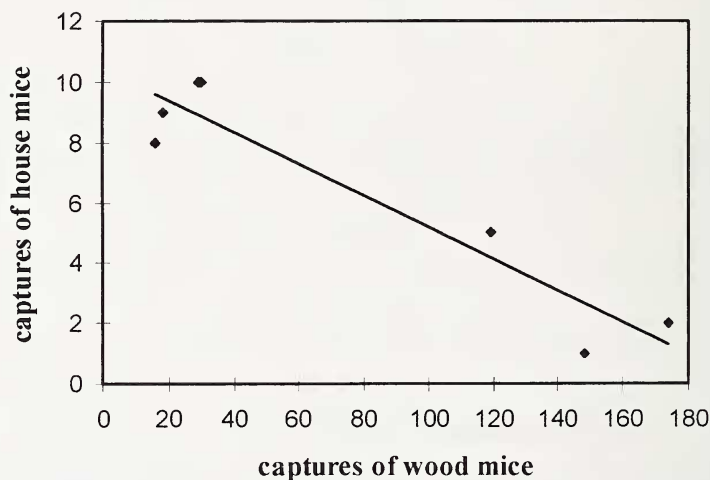

Fig. 2. The relationship between the number of captures of wood mice and house mice at trap points outside building sites surrounded by vegetation. There was a significant negative correlation between captures of house mice and captures of wood mice (r = –0.945, df = 5, p < 0.01).

No relationship between numbers of captures of wood mice and house mice was found at woodland sites. However, wood mice were more likely to use woodland stacks when house mice were absent than when they were present: a significantly greater proportion of wood mouse captures occurred in stacks when house mice were absent (F$_{(1,12)}$ = 12.99, p = 0.004).

Predation

There was evidence of much higher predation levels at woodland sites than in buildings. Domestic cats were infrequently present at two building sites, and fox prints were occa-

sionally found inside a third. In contrast, both indirect signs (scats and paw prints) and direct sightings showed that weasels (*Mustela nivalis*), badgers (*Meles meles*), foxes (*Vulpes vulpes*), and tawny owls (*Strix aluco*) were present at all woodland sites. Eight stacks were dismantled in woodland and eight in buildings. While there were no signs of predation in building stacks, four (50%) of those dismantled in woodland contained weasel nests and scats. Weasels were twice accidentally captured in woodland stacks.

Discussion

Once an area has been reached, in our case by artificial translocation, successful establishment could be prevented by breeding failure or by short residency of immigrants. Residency could be reduced by emigration or death, for example in response to competition or predation. DONCASTOR (1992) has shown how predation influences where hedgehogs (*Erinaceus europaeus*) live. Hedgehogs transplanted into woodlands containing high densities of predators (badgers) suffered higher mortality and dispersed away from their release sites at greater rates than hedgehogs introduced into woodland without predators.

In apparently suitable habitats poor breeding success and/or short residency, could result from resource or interference competition (DE LONG 1966; LIDICKER 1966). Resource competition with wood mice was implicated by BERRY and TRICKER (1969) as a reason for the extinction of the house mouse on the Scottish island of St. Kilda when the human population left. Bearing in mind that house mice are not indigenous over most of their geographic range, they are likely to be prone to competition from other small mammals, which may be more finely adapted to local conditions. Indeed, permanent populations of house mice are most common in areas where there are empty niches, such as species-impoverished islands (e. g. BERRY 1964; BERRY et al. 1979; DUESER and PORTER 1986; GRANJON and CHEYLAN 1988) or land disturbed by agriculture, mining or fire (e. g. Fox and Fox 1986; BREISE and SMITH 1973; STICKEL 1979). In reciprocal removal experiments Fox and POPLE (1984) and Fox and GULLICK (1989) have shown that house mice are competitively inferior to the Australian *Pseudomys novaehollandiae*, except at very high densities.

Our experiments suggest that in the success or failure of establishment of house mouse populations in buildings and woodland depends, at least in part, on a subtle interaction between competitive exclusion by wood mice and predation, predominantly by weasels.

ADAMKZYK and RYSKOWSKI (1965), and LIDICKER (1976), found that after introduction to an attic and enclosure respectively, house mice ranged widely initially, and then quickly showed strong site preferences. In our study, larger numbers of captures away from the stacks in buildings than in woods suggest that differences in losses of animals between the time of introduction and the first trapping session may be due to greater initial movement from buildings during the settling-in phase.

Subsequent establishment of some populations of introduced house mice in the vicinity of the buildings suggests that differences in capture rates away from stacks reflect a spreading out from the stack rather than dispersal away from the site. In the woods there was little evidence of emigration, with the majority of animals being caught in or around the stack. One exception was site 13, which had little canopy cover, but had particularly good ground cover, with a lattice-work of dead wood covered with cleavers (*Galium aparine*) surrounding the stack, which clearly aided movement of animals. However, seven of the eight individuals caught outside were subsequently recaptured in the stack. This provides further evidence that there truly was little emigration from woodland sites, rather than that emigrating animals dispersed away from an area very quickly and so were difficult to trap (WALKOWA et al. 1989).

Differences in movement away from the stacks may have resulted in different spatial groupings, with house mice in woods living closer together, packed into the stack, and house mice in buildings being more scattered. Such spatial differences might affect aspects of social organisation, such as levels of aggression and reproduction (PELIKÁN 1981; WALKOWA 1981), leading to the lower rates of recruitment observed in woodland. However, differences in the number of young conceived in buildings and woodland could also be an artefact of low adult survival in woodland.

Another, more severe, consequence of the spatial organisation of house mice in woods seems to have been increased vulnerability to extinction from predation. A small, sedentary group of house mice living at high density, as they were in woodland, would – once they had been found by a predator – be more susceptible to predation than scattered, mobile groups such as those in buildings. A small, nimble predator such as a weasel, which could enter the very heart of a stack, could easily and quickly kill the majority of the group. Our evidence shows that not only did weasels enter stacks, but they also made their nests in them.

Why did house mice in buildings move out of stacks, while house mice in woodland did not? One of the main differences between building and woodland sites was that there were far fewer predators present in the buildings. LIMA and DILL (1990) argue that there is evidence that animals are able to asses their risk of predation, and make decisions about their feeding, social, or escape behavior accordingly. In woodland the presence of predators outside the stacks, and the lack of evidence for prior predator visits within the stacks, may have reduced the apparent risk of predation to mice which remained within the stacks. In buildings, where few or no predators were present, the risks from predation would have been similar in and out of the stacks.

A second difference was that there were no wood mice in the buildings, although they were present outside. Evidence from building sites indicates that movement of house mice was restricted by the presence of the abundant wood mice. At building sites house mice moved outside despite the presence of wood mice, but there was a negative correlation between captures of wood mice and house mice outside buildings. This correlation suggests either that house mice were not moving outdoors in areas where wood mouse numbers were high, or that there was competition for traps. However, the large number of wood mouse captures compared to house mouse captures, and the fact that at least 50% of traps remained unsprung each morning, support the idea that house mice actively avoided wood mice.

We have shown that even when provided with sufficient food and shelter, and artificially translocated in groups, house mice are unable to colonise English woodlands but colonise derelict buildings with ease. Large-scale ecological experiments in the field are extremely difficult, being costly, time-consuming, and hard to control. While our design allowed direct comparison of establishment success of house mice in buildings and woodland, it did not allow us to rigorously test for the effect of competition and predation. None the less, our data allow us to suggest that woodland was unsuitable for house mice due to an interplay between competition and predation: competition with wood mice restricted house mice to their focal introduction point making them vulnerable to extinction through predation by weasels. Experimental manipulations of house mice and their competitor and predator densities are required to fully test their effect on house mouse colonisation. However, our preliminary data point to some of the potential problems encountered by colonists and are relevant to wider question of how animals are distributed in space.

Acknowledgements

Zusammenfassung

Experimentelle Kolonisation von gegensätzlichen Habitaten durch Hausmäuse

Hausmäuse (*Mus domesticus*) sind erfolgreiche Kolonisten. Sie besiedeln viele verschiedene Habitate und leben sowohl in Gebäuden als auch im Freien, generell jedoch nicht in Waldgebieten. Wir haben einige der Prozesse und Faktoren untersucht, die die erfolgreiche Besiedlung durch Hausmäuse beeinflussen, indem wir das Schicksal von Mäusen, die in Waldgebieten ausgesetzt wurden, mit dem von Mäusen verglichen haben, die in Gebäuden ausgesetzt wurden. Beiden Gruppen wurde jeweils an einem bestimmten Fokuspunkt Nahrung und Schutzmöglichkeit (Strohhaufen) angeboten. Während sich Hausmäuse in Gebäuden generell etablierten und fortpflanzten, starben die Hausmäuse im Wald innerhalb von drei Monaten wieder aus. Hausmäuse in Gebäuden verbreiteten sich ausgehend von den Strohhaufen und siedelten sich zum Teil im umliegenden Grasland an, während Hausmäuse in Waldgebieten die Strohhaufen nur selten verließen. In der Umgebung von Gebäuden korrelierte die Anzahl gefangener Hausmäuse negativ mit der Fangquote von Waldmäusen (*Apodemus sylvaticus*). In Waldgebieten, nicht jedoch in Gebäuden, wurde ein starker Beutedruck von Mauswieseln (*Mustela nivalis*) auf Hausmäuse beobachtet. Wir folgern, daß aufgrund einer Kombination von Konkurrenz- und Beutedruck Waldgebiete für Hausmäuse ungeeignet waren: Konkurrenz mit Waldmäusen beschränkte Hausmäuse auf das Gebiet, in dem sie ursprünglich freigelassen wurden und machte sie damit anfällig für Ausrottung durch Beutedruck von Mauswieseln.

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